Deviations from strict *M* scaling

P. Bijl,* J. J. Koenderink, and A. M. L. Kappers

Buys Ballot Laboratory, Utrecht Biophysics Research Institute, University of Utrecht, P.O. Box 80.000, 3508 TA Utrecht, The Netherlands

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It has been hypothesized that the visibility of stimuli can be made independent of location in the visual field if they are scaled according to the cortical magnification factor *M* (*M* scaling) [Exp. Brain Res. **37,** 495 (1979); J. Opt. Soc. Am. A **4,** 1568 (1987)]. Although the predictions of this hypothesis are quite good with regard to contrast sensitivity for sine wave gratings, they are inaccurate with regard to the detection of circular disks: the visual field contains large regions where diameter-threshold curves for these stimuli are independent of retinal location [Am. J. Optom. **49,** 748 (1970); Vision Res. **20,** 967 (1980)], although *M* varies by a factor of 3 over these regions. We measured diameter-threshold functions for circular symmetric stimuli with a Gaussian luminance profile and Gaussian temporal modulation at various eccentricities (as high as 42°) along both sides of the horizontal meridian. Along the temporal side the results are similar to those for disks: between 12° and 42° the curves are largely independent of eccentricity. In addition a strong nasotemporal asymmetry is found: for the nasal side the thresholds are considerably higher than for the temporal side. The results suggest both scale and gain differences over the visual field. Reanalysis of data for gratings shows that *M* scaling holds only for high spatial frequencies at which the slope of the contrast sensitivity function is steep (acuity); if the slope is less steep, the results are similar to those for localized stimuli. The results can be explained if we assume that (i) the spatial scale varies proportionally to the diameter of the smallest receptive field center and (ii) the gain is a function of the overlap factor, i.e., the number of retinal ganglion cells covering a single point in visual space.

INTRODUCTION

In many respects human photopic vision is superior in the fovea relative to the periphery. However, it has been shown that for many (psychophysical) tasks this difference is of a quantitative rather than a qualitative nature, caused merely by scale differences at, for instance, the retinal ganglion cell level or by different values of the cortical magnification factor *M* [the linear extent of the visual striate cortex (in millimeters) representing each linear degree of visual field]. For example, Cowey and Rolls[1] show that visual acuity is directly proportional to *M*. Koenderink *et al.*[2] show that contrast detection thresholds for moving sine wave gratings at the fovea and at various eccentricities along the nasal horizontal half-meridian of the visual field become identical if the just-resolvable distance (the reciprocal of acuity) is taken as a measure to scale the stimulus. Similarly, Rovamo *et al.*[3-5] show that contrast thresholds for detection and discrimination of sinusoidal gratings are quite independent of retinal location if the stimuli are scaled proportionally to M^{-1} (*M* scaling). They proposed an elegant hypothesis that predicts equal thresholds for visual stimuli across the visual field if the calculated cortical representations of these stimuli are equivalent. This hypothesis, which was later called the cortical magnification theory of peripheral vision,[6] has been verified for a wide variety of psychophysical tasks, although failures have also been reported (for an overview see, e.g., Pointer[7] and Virsu *et al.*[6]; also see Strasburger *et al.*[8]).

One of the failures concerns the detection of sharp-edged disks. Harvey and Pöppel[9] show that the contrast detection threshold for a 10'-diameter circular disk increases between the fovea and ~10° but is constant in a region that extends from 10° to 35° in the temporal visual field and from 10° to 20° in the superior, the inferior, and the nasal visual fields. For larger eccentricities the threshold increases again. This result is confirmed for the horizontal meridian by Lie,[10] Johnson *et al.*,[11] and Fahle and Schmidt,[12] although in the last-named two studies the boundaries of the plateau and the large nasotemporal asymmetry are less pronounced. Lie presents complete diameter-threshold functions: sensitivity can be made independent of retinal location by scaling of the stimuli, but the scaling factor is independent of eccentricity in the regions mentioned above, although M^{-1} increases by a factor of 3 in the same region on the temporal side. At the nasal side the differences in the results for gratings and disks are less striking: on this side the plateau for disks is small or even absent.[13]

To find the origin(s) of the above-mentioned differences, we measured diameter-threshold functions for stimuli with a Gaussian luminance profile and Gaussian temporal modulation presented on a large uniform-background field. Similar to gratings but in contrast to disks, these stimuli do not have abrupt transitions in space or time. On the other hand, in contrast to gratings and similar to disks, they are essentially two dimensional and localized, do not extend over a large part of the visual field, and contain a net flux. In addition, some measurements were carried out with a localized stimulus that contains no net flux. The data may reveal the cause of the different results for gratings and disks.

The experimental method we used differs fundamentally from the one usually applied to test the cortical magnification theory. In most of the experiments the applicability of the theory to a specific task is tested in an indirect way: the stimulus is scaled according to a prior estimate of *M*

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(usually the estimates made by Rovamo and Virsu[3] are used), and afterward the investigators check whether performance is independent of location in the visual field. However, the optimal scaling factor depends on the subject and the specific task. If, after scaling, performance varies across the visual field, this may be due either to a wrong scaling factor or to a failure of the theory. This means that the theory can be neither accepted nor rejected. If, on the other hand, performance is more or less equal at different locations, we have no measure of how critically the results depend on the scaling factor, and failures or deviations of the theory may remain hidden.

The method we used is similar to the one used by Wilson,[13] Johnston,[14] and Lie[10]: all the stimuli at one retinal location are simply magnified versions of one another. As is pointed out by Watson,[15] with this method the cortical magnification theory can be tested without prior knowledge of a scaling factor: the theory holds if and only if the diameter-threshold curves (plotted on a log axis) are of similar shapes and are simply shifted horizontally with respect to one another. In that case the experiment yields the required scaling factor (the horizontal shift). If the theory does not hold, the deviations (and their effect) are rendered unambiguously.

Another advantage is that we presented the stimuli on a large uniform-background field; only stimulus size was varied. Magnification of both stimulus and background size changes the total amount of light reaching the eye, thus influencing pupil diameter, optical performance of the eye, and mean retinal illuminance.[6] If, on the other hand, the size of a restricted background field is fixed, edge effects may influence the visibility for the largest stimuli.[16] Owing to scale differences among different locations it is in this case impossible to test the theory for large targets.[15]

METHODS

Initial Experiments

For three subjects, MA, NR, and PB, we determined the position of the blind spot by using a perimeter to make sure that the stimuli were not presented (partially) in this region.

In addition, we measured the minimal angle of resolution (MAR) for a 100%-contrast sine wave grating at eccentricities between the fovea and 48° along the temporal meridian of the visual field. The results for the three subjects are very similar: the MAR increases approximately linearly with eccentricity over the entire range. Quantitatively, the results are comparable with data presented by Weymouth.[17]

Experimental Setup

In the contrast detection threshold experiments the stimuli were presented on a large uniform-background field. The experimental setup is described in detail elsewhere.[16,18] The basic concept is as follows: the subject views a monochrome cathode-ray tube (CRT) through a circular aperture in a homogeneously illuminated background screen of 110° × 70°. The background screen and the CRT have the same luminance and apparent color. The screen is placed much closer to the subject than the CRT. If the subject's eye is focused on the CRT, the edge of the aperture is out of focus and hardly affected by small accommodation fluctuations, so the CRT gradually merges with the background screen. With a good fixation, no transition is visible. For foveal and near-peripheral viewing, a small black fixation spot (diameter 2′) is placed on the CRT; for larger eccentricities, the fixation spot is placed on the background screen and a lens is used to make the subject's eye accommodate to the correct distance.

To obtain the same apparent color for the CRT and the background screen, one places a red filter in front of the subject's eye. The additional advantage is that mainly one class of receptor, namely, the red-sensitive cones, is stimulated. This prevents the mixing of different magnification functions for different retinal cell types.[19] On the other hand, retinal illuminance is reduced to ~100 Td, which is near the lower limit of the photopic region for the fovea. Control experiments, in which the color filter had been removed (luminance ~15 times higher), showed that, for most stimuli, thresholds do not depend markedly on luminance. For the largest stimuli, edge effects[16] are found if the filter is absent, since the color difference makes the transition from CRT to background visible.

Measurement Procedure

The measurement procedure is described elsewhere.[18] An initial estimate of the threshold is obtained by using a Yes–No staircase procedure; a final estimate is obtained with a two-alternative forced-choice procedure. Each measurement is repeated three to six times, yielding a standard deviation of ~10%.

Five subjects participated in the experiment. Each of the subjects used the dominant (right) eye. Subjects NR, AK, and LM are emmetropic; subjects MA and PB are slightly myopic and used their spectacles for optical correction.

Stimulus

Two types of stimulus were used. Extensive experiments were carried out with an isotropic stimulus with a Gaussian luminance profile and Gaussian temporal modulation (circular Gaussian blob) presented on a steady background. The luminance of this stimulus at time t at a distance r from the stimulus center is given by[20]

$$L(r,t) = L_b + L_0 \exp\left[-\frac{r^2}{2\sigma_s^2} - \frac{(t-t_0)^2}{2\sigma_t^2}\right], \quad (1)$$

where L_b is the background luminance and L_0 is the maximum luminance difference between the stimulus and the background in both space and time. The diameter of the stimulus is defined as two times its width σ_s measured in visual angle. σ_t is the presentation time.

Some experiments were carried out with a stimulus that contains no net flux (Mexican hat). Its luminance profile is given by the normalized Laplacian of a two-dimensional Gaussian function:

$$L(r,t) = L_b + L_0\left(1 - \frac{r^2}{2\sigma_s^2}\right)\exp\left[-\frac{r^2}{2\sigma_s^2} - \frac{(t-t_0)^2}{2\sigma_t^2}\right]. \quad (2)$$

The contrast of the stimuli is defined as

$$\text{contrast} = (L_0/L_b) \times 100\%. \quad (3)$$

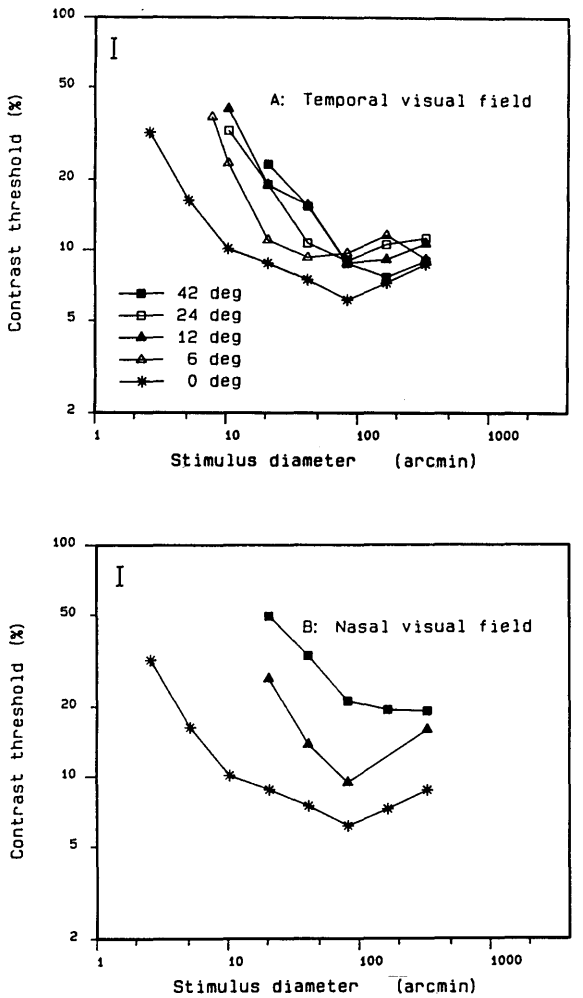

Fig. 1. Diameter-threshold functions for $\sigma_t = 0.50$ s. Subject MA. A, Temporal horizontal half-meridian of the visual field. We can make the curves coincide by using a horizontal shift. B, Nasal half-meridian. It is impossible to make the curves coincide by using a horizontal shift only.

RESULTS

The measurements for Gaussian blobs were carried out at the fovea; at 6°, 12°, 24°, and 42° along the temporal horizontal half-meridian; and at 12° and 42° along the nasal horizontal half-meridian of the visual field. The largest stimulus diameter was 5.5° at all the eccentricities; the diameter of the smallest stimulus was limited by the highest contrast that can be generated by the setup (~60%, see Ref. 16) and increased from 2.6′ at the fovea to 20.7′ or 41.4′ at the highest eccentricities. For stimuli with a diameter larger than or equal to 20.7′ the monitor was placed at a distance of 0.65 m. For stimuli smaller than or equal to 41.4′ the monitor was placed at a distance of 2.60 m. Thresholds for stimuli with the same angular diameter showed no systematic dependence on viewing distance. In the figures only their averages are plotted.

Two presentation times were used: $\sigma_t = 0.50$ s and $\sigma_t = 0.13$ s. Bijl *et al.*[16] showed that the detection of circular Gaussian blobs at the fovea may be divided into two classes on the basis of their presentation times: if the presentation time is long ($\sigma_t = 0.50$ or 1.0 s), the stimuli are detected mainly on the basis of their spatial properties. If the presentation time is shorter ($\sigma_t = 0.13$ or 0.25 s), the temporal properties of the stimulus play a role as well.

Extensive data sets were gathered for subjects MA, NR, and PB. Control experiments were carried out for the other subjects to confirm the most important results. The results for four subjects, MA, NR, AK, and LM, are similar. In some respects the results for subject PB differ significantly for the temporal side of the visual field (see below). Figures 1 and 2 show the results of the measurements for subject MA for $\sigma_t = 0.50$ s and $\sigma_t = 0.13$ s, respectively. The thresholds are plotted as a function of the stimulus diameter. At all eccentricities the curves consist of two parts: for relatively small stimuli the thresholds decrease rapidly with the stimulus diameter (partial spatial summation); for large stimuli the curves are rather flat. We previously reported these results for Gaussian blobs at the fovea.[16] Within the experimental errors the shape of the curves is independent of the location of the stimulus; the diameter at which the transition takes place depends on eccentricity and presentation time.

The thresholds for all the stimuli are lowest at the fovea and generally increase with eccentricity. Only the thresholds for the large stimuli (diameter larger than ~1°) along the temporal meridian (Figs. 1A and 2A) do not de-

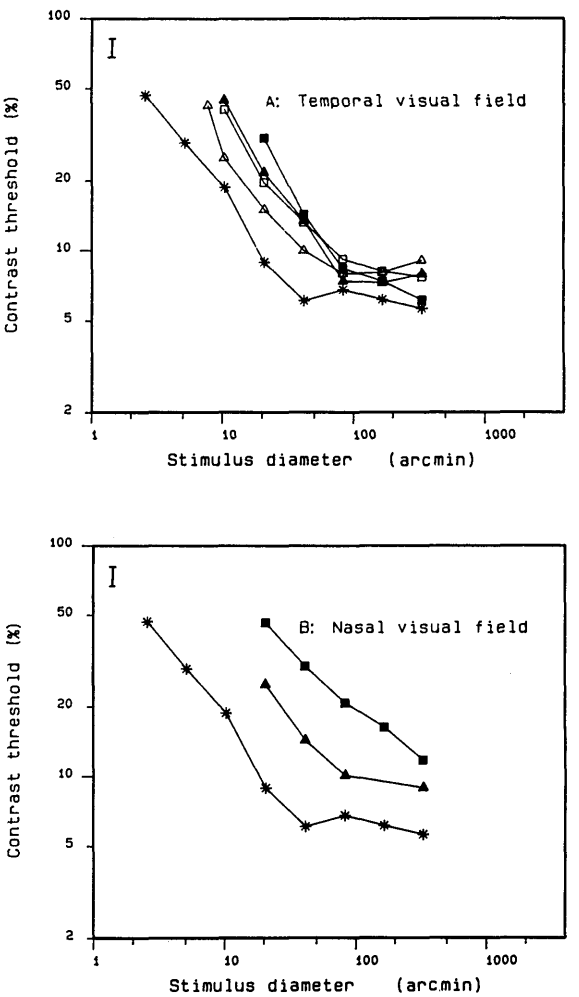

Fig. 2. Diameter-threshold functions for $\sigma_t = 0.13$ s. Subject MA. The symbols are as in Fig. 1. The results are similar to those for $\sigma_t = 0.50$ s.

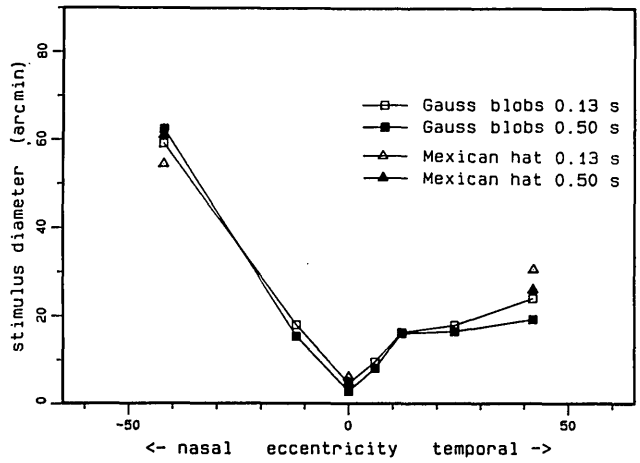

Fig. 3. Cross section of the diameter-threshold curves through the 25%-contrast level as a function of eccentricity. The nasotemporal asymmetry is pronounced: on the nasal side the stimulus diameter increases rapidly with eccentricity; on the temporal side it remains remarkably constant between 12° and 42°.

pend significantly on eccentricity. For this meridian, we can make all threshold-diameter curves coincide by using a horizontal shift only. This means that the visibility of all the stimuli can be made independent of eccentricity if their diameters are scaled according to a single factor. Such a scaling operation leaves only a small residual effect: the thresholds for the large stimuli at the fovea are in general slightly lower than those at other locations.

For the nasal meridian (Figs. 1B and 2B) the curves are of similar shapes, but a horizontal shift is insufficient to make the curves coincide. This is shown most clearly for $\sigma_t = 0.50$ s, at which the constant-threshold level for the large stimuli increases considerably with eccentricity. It is possible, however, to make the curves coincide if we permit both a horizontal and a vertical shift to occur. In that case we define simultaneously two factors that apply to all the stimuli at one retinal location: one factor is concerned with scale, and the other is concerned with relative sensitivity or gain. Note also that the curves for the same eccentricities on opposite sides of the fovea are shifted mainly vertically with respect to one another, indicating that gain, not scale, is the main difference. We will return to this in the Discussion.

The nasotemporal differences (and similarities) are shown clearly if we calculate the stimulus diameters at which the curves in Figs. 1 and 2 intersect a fixed contrast level. At the same time, we obtain an objective measure of the horizontal shift that is required for the curves for the temporal meridian to coincide. At high contrast levels small errors in diameter are obtained owing to the steepness of the curves. In Fig. 3 the cross sections of the curves with the 25%-contrast level (obtained by linear interpolation between two adjacent data points) are plotted as a function of eccentricity for the two presentation times. The data points represent the (geometrical) mean of the values for all the subjects except subject PB. The spread between the data points for different subjects is very small (the average spread is ~0.07 log unit).

The results are similar for both presentation times. Figure 3 shows that, for eccentricities less than 12°, diameters increase similarly along both half-meridians. At higher eccentricities, however, the nasotemporal asymmetry is very pronounced: at the nasal side the stimulus diameter increases rapidly with eccentricity up to 42°; at the temporal side it remains remarkably constant between 12° and 42° eccentricity (the diameter at 42° is ~1.4 times the diameter at 12°, averaged over all the subjects and two presentation times). Thus along this half-meridian the performance of the visual system in this detection task is nearly constant over 30°. Cross sections through lower-contrast levels yield even larger nasotemporal differences.

For two subjects, MA and NR, we repeated the experiments for small stimuli with the Mexican hat luminance profile. The measurements were carried out for the fovea and for 42° on both sides of the horizontal meridian, and the cross sections with the 25%-contrast level were obtained. Again these values are determined accurately, owing to the steepness of the diameter-threshold function at this level, and the intersubject variation is very low (average spread 0.03 log unit). In Fig. 3 the average values for the two subjects are plotted. The results are similar to those for Gaussian blobs and again show a large nasotemporal asymmetry.

At the fovea and on the nasal side of the visual field the data for subject PB agree well with those for the other subjects, except that his thresholds are systematically somewhat lower. In contrast to the results for the other subjects, his results show a large degree of symmetry: for both the nasal and the temporal sides the constant-threshold level increases with eccentricity. Thus for subject PB it is impossible to make the curves for both sides of the horizontal meridian coincide by using a horizontal shift. Similar results were obtained when this subject used his left eye.

DISCUSSION

The most important conclusions based on the results of our experiments are as follows:

- The detection of circular blobs with a Gaussian luminance profile and a Gaussian temporal modulation along the horizontal meridian of the visual field shows a large nasotemporal asymmetry for eccentricities larger than 12°.
- For the temporal side it is possible to define a single scaling factor that makes visibility independent of eccentricity over the entire range of stimulus sizes. This factor increases rapidly with eccentricity between 0° and 12° but remains remarkably constant between 12° and 42° eccentricity. After scaling, only foveal thresholds (for large blobs) are slightly lower.
- For the nasal side it is impossible to define a scaling factor that makes visibility independent of eccentricity: the constant-threshold level for large stimuli increases considerably with eccentricity. Making the curves for different eccentricities coincide requires both a horizontal and a vertical shift.
- The results for small stimuli with a Mexican hat luminance profile containing no net flux, presented at the fovea and at 42° along both sides of the horizontal meridian, are similar to those for Gaussian blobs.

According to the cortical magnification theory, a single scaling factor, increasing approximately linearly with ec-

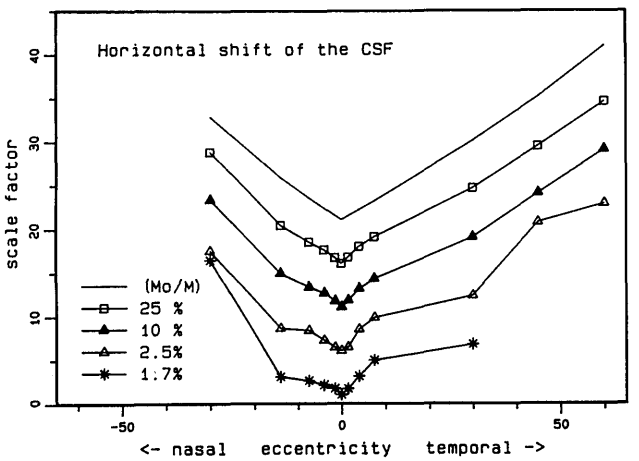

Fig. 4. Cross sections of the CSF's[3] through several contrast levels, normalized at the fovea, together with the estimate of (M_0/M). The curve for the 1.7%-contrast level is positioned correctly; all the other curves are displaced vertically for clarity. For high contrast levels the scale factor equals (M_0/M); for low levels a plateau is found just as it is for localized stimuli.

centricity, can make all the diameter-threshold curves coincide. Obviously, the theory cannot account for the results outlined above.

For the temporal side of the visual field the results for Gaussian blobs and the Mexican hat stimuli are similar to those reported earlier for disks.[9,10] Thus along this half-meridian large differences in the spatial and the temporal properties of localized stimuli do not influence the scaling factor required for making thresholds equal for different eccentricities. Apparently, the different results for gratings and disks at retinal locations beyond the blind spot are a consequence neither of the abrupt transitions of disks in space or time nor of their net flux. Our next step is to analyze the contrast sensitivity functions (CSF's) determined by Rovamo and Virsu[3] in a way similar to that which we applied to our data: for the locations along the horizontal meridian (their Figs. 4a and 4b) we determine the (highest) spatial frequency that corresponds to a fixed contrast level. The results are expressed in terms of a scaling factor relative to the fovea. In Fig. 4 the scaling factors are plotted as a function of eccentricity for four different threshold levels: 25%, 10%, 2.5%, and 1.7% (for the 25%-contrast level some estimates are obtained by extrapolation), together with their estimate for (M_0/M), where M_0 is the value of M at the fovea. It should be noted that thresholds for gratings are approximately 1 order of magnitude lower than for Gaussian blobs.[16,21] It is clear that the shape of the curves in Fig. 4 changes systematically with the contrast level: at high levels the scaling factor varies linearly with (M_0/M), similar to the inverse of acuity (which is a cross section at 100%). The lower the threshold, however, the more the curves show a plateau in the regions where a plateau is found for localized stimuli. We conclude that the cortical magnification theory holds for the detection of gratings at high threshold levels (acuity) but that at lower thresholds it does not apply any more consistently to gratings than it does to localized stimuli.

For the nasal side of the horizontal meridian we report another shortcoming of the cortical magnification theory: the threshold level for large Gaussian blobs presented peripherally is essentially higher than at the fovea (especially for slowly varying blobs) or at corresponding eccentricities along the temporal side of the meridian. There is no scaling factor that can compensate for this loss in sensitivity. Recently similar results were reported by Valeton and Watson[22] for both Gaussian blobs and Gabor patches for different temporal frequencies at near eccentricities (0–16°) along the nasal half-meridian. They also used a method to test the cortical magnification theory in a direct way (proposed by Watson[15]) and found that matching the curves for different eccentricities requires both a horizontal and a vertical shift.

A simple phenomenological model can account both for the strong nasotemporal asymmetry that we find and for the different results for gratings at different threshold levels. In this model we permit both a horizontal (scale) and a vertical (gain) shift to occur. The model assumptions are as follows:

- The spatial scale varies proportionally to the diameter of the smallest receptive field center.
- The gain is a function of the overlap factor, i.e., the number of retinal ganglion cells covering a single point in visual space or, equivalently, the ganglion cell density times the mean receptive field area.

Recently Wässle *et al.*[23] showed that for the macaque monkey the areal cortical magnification factor (M^2) is directly proportional to the retinal ganglion cell density. Thus the second assumption is equivalent to stating that gain is a function of the point-image size, i.e., the area of striate cortex subserving a single point in visual space.

Neither the diameter of the receptive field center nor the overlap factor as a function of retinal location is known accurately for the human visual system. We therefore approximate the spatial scale in the following way: According to the model, CSF's or diameter-threshold curves for different locations in the visual field are shifted both horizontally (scale) and vertically (gain) with respect to one another. However, when the CSF is steep, gain differences only slightly influence the curves, and the horizontal (scale) shift directly follows from the data. Thus, as a first-order approximation, we may assume that the spatial scale (and the diameter of the smallest receptive field center) varies proportionally to the MAR, which in turn is directly proportional to the estimate of (M_0/M) by Rovamo and Virsu[3] (see Fig. 4). In the cortical magnification theory this is the only variable: a constant gain is assumed. Our model further takes into account the fact that the decrease in the ganglion cell density and the increase in the receptive field area toward the periphery are not in balance, as is shown below. To approximate the course of the overlap factor we assume first that the ganglion cell density for the human visual system varies with eccentricity in the same way as it does for the visual system of the macaque monkey, as estimated recently by Wässle *et al.*[23] Second, we assume that the ratio between the surround and the center diameter of the receptive fields is approximately constant over the visual field. In that case the overlap factor varies approximately as the product of the cell density and $(M_0/M)^2$. In Fig. 5 the overlap factor thus obtained is plotted (normalized at the fovea) as a function of eccentricity. The overlap factor shows a local maximum at the fovea and is comparable for

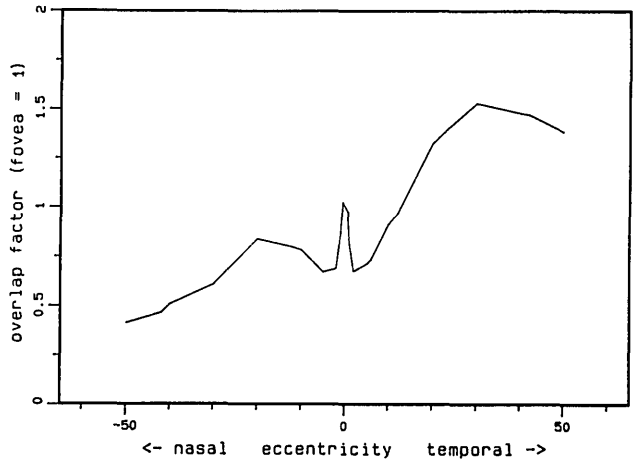

Fig. 5. Estimate of the human retinal overlap factor, normalized at the fovea, as a function of eccentricity. See the text for details.

the nasal and the temporal sides if the eccentricity is less than ~10° but is largely different for higher eccentricities (the difference increases up to approximately a factor of 3 for eccentricities greater than 30°.

In Fig. 6 we have plotted the diameter-threshold curve for Gaussian blobs at the fovea (subject MA, $\sigma_t = 0.50$ s) together with predictions for peripheral locations derived from this curve by multiplying all stimulus diameters by (M_0/M) (scale shift) and dividing the thresholds by the overlap factor given in Fig. 5 (gain shift). The choice of the relationship between the overlap factor and the gain is discussed below. Despite the rough estimates of the receptive field size and the overlap factor, the predictions agree well with the experimental results presented in Fig. 1. The local maximum of the overlap factor at the fovea may account for the slight superiority that is left after horizontal scaling. For the nasal side of the visual field the overlap factor is always smaller than at the fovea, which explains the vertical threshold shift that is found for this half-meridian. For the temporal side the overlap factor increases rapidly between 5° and 30°. The combined effect of the scale shift to the right and the gain shift downward means that thresholds are rather independent of eccentricity between 12° and 42°. Finally, the model explains why curves for the same eccentricities on opposite sides of the fovea are shifted mainly vertically with respect to each other.

For subject NR similar results were obtained for both presentation times. The predictions for subject MA with $\sigma_t = 0.13$ s agree less well because of the atypical shape of the diameter-threshold curve for the fovea. However, if we start from a different curve the predictions are again satisfactory.

What is the mathematical relationship between gain and the overlap factor? In earlier experiments[2,18] it was found that contrast sensitivity to gratings and to elliptical Gaussian blobs varies approximately as the square root of the number of ganglion cells that are activated. The present data (for both subjects, two presentation times) are predicted best if we assume a power function with a slightly higher exponent (between 0.5 and 1). However, the exact value of the exponent is of little significance because it is based on rather coarse model assumptions. For at least two reasons the MAR can be used only as a first-order approximation for the spatial scale and the receptive field center diameter. First, the MAR overestimates the diameter at the fovea because the optical degradation of the eye is relatively largest in that region. Second, according to the model, the MAR depends on both scale and gain. If the gain is low, the MAR is shifted to higher spatial frequencies, and the receptive field diameter is relatively overestimated; if the gain is high, the diameter is underestimated. An incorrect estimate of the diameter influences both the horizontal and the vertical shift. Furthermore, we have assumed that the ratio between the surround and the center diameter of the receptive fields is constant over the visual field. For ganglion cells in the cat retina there are indications that this ratio decreases with eccentricity.[24] Finally, we have assumed that the density of human retinal ganglion cells is the same as that for the macaque.

The model also accounts for the results obtained for gratings (shown in Fig. 4). If the CSF is not steep (i.e., at low contrast levels), cross sections with a fixed contrast

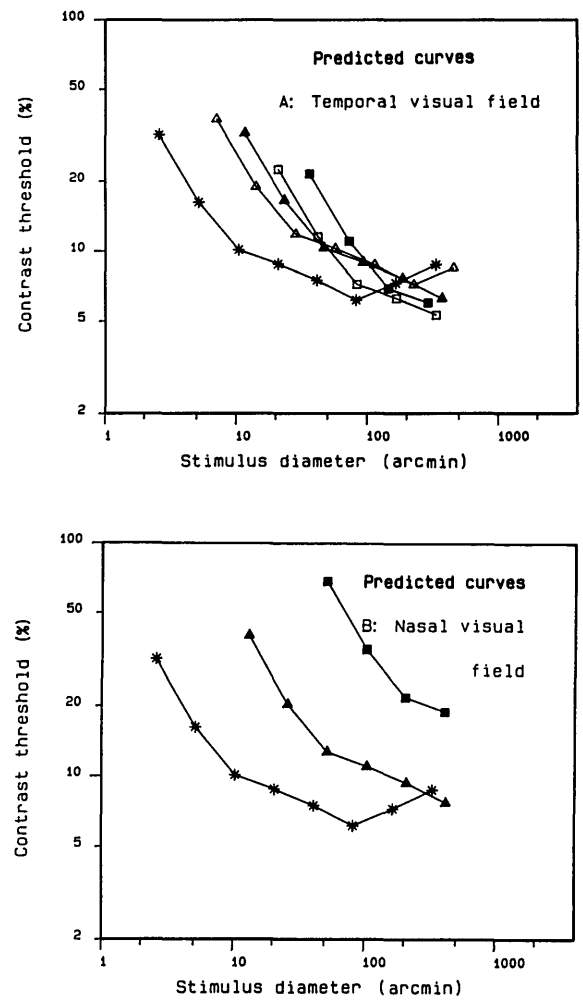

Fig. 6. Predicted diameter-threshold functions for Gaussian blobs along the horizontal meridian, derived from the curve for the fovea (subject MA, $\sigma_t = 0.50$ s) by multiplying all stimulus diameters by (M_0/M) (scale shift) and dividing the thresholds by the overlap factor given in Fig. 5 (gain shift). The symbols are as in Fig. 1. The combined effect of a scale-and-gain shift means that for the temporal side the thresholds depend less on eccentricity than expected on the basis of the cortical magnification theory. For the nasal side the opposite holds.

level are determined by both local scale and gain, and results similar to those for localized stimuli are expected. However, if the CSF is steep, cross sections are determined primarily by scale and only slightly by gain. This means that in this region the results can be explained equally well with a model that takes only scale differences into account and that the MAR varies roughly according to the local spatial scale (and approximately linearly with eccentricity). The present model can account for the different results for subject PB for Gaussian blobs if we assume that in his case the ganglion cells are distributed somewhat differently. If they are, this will hardly influence the predictions for the MAR. Thus the MAR for this subject is expected to be similar to those for the other subjects, as is indeed the case.

In summary, cortical magnification theory in its simplest form is unable to explain a variety of phenomena that take place at the contrast detection threshold. A simple extension of the cortical magnification theory that takes into account that the gain of the visual system varies over the visual field (being a function of the overlap factor) explains the following effects:

- At the fovea performance is slightly superior to that in surrounding regions, even after correction for scale differences.
- Below ~10° nasotemporal differences are small; at higher eccentricities the differences in threshold are determined almost entirely by gain differences (curves shifted vertically with respect to one another).
- In the region between 10° and 35° along the temporal half-meridian the diameter-threshold curves for localized stimuli are quite independent of eccentricity owing to a combined effect of both scale and gain differences. Similar effects occur for sine wave gratings if the CSF is not too steep.
- The MAR varies approximately linearly with eccentricity. Similar results are expected for other tasks in which gain is unimportant.

There is one effect that cannot be explained straightforwardly: whereas the results for Gaussian blobs and Gabor patches[22] clearly point in the direction of a gain loss along the nasal half-meridian, diameter-threshold functions for sharp-edged disks match optimally if they are shifted only horizontally.[10,13] For example, not only is the threshold level for large stimuli independent of retinal location but so is the threshold at which Ricco's law (complete spatial summation) breaks down. Probably these stimuli activate (partly) different mechanisms owing to their sharp edges in either space or time. If these mechanisms are distributed differently in the visual field, different results are expected.

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*Present address, TNO Institute for Perception, P.O. Box 23, 3769 ZG Soesterberg, The Netherlands.

REFERENCES AND NOTES

1. A. Cowey and E. T. Rolls, "Human cortical magnification factor and its relation to visual acuity," Exp. Brain Res. **21,** 447–454 (1974).
2. J. J. Koenderink, M. A. Bouman, A. E. Bueno de Mesquita, and S. Slappendel, "Perimetry of contrast detection thresholds of moving spatial sine wave patterns. III. The target extent as a sensitivity controlling parameter," J. Opt. Soc. Am. **68,** 854–860 (1978).
3. J. Rovamo and V. Virsu, "An estimation and application of the human cortical magnification factor," Exp. Brain Res. **37,** 495–510 (1979).
4. J. Rovamo, V. Virsu, and R. Näsänen, "Cortical magnification factor predicts the photopic contrast sensitivity of peripheral vision," Nature (London) **271,** 54–56 (1978).
5. V. Virsu and J. Rovamo, "Visual resolution, contrast sensitivity, and the cortical magnification factor," Exp. Brain Res. **37,** 475–494 (1979).
6. V. Virsu, R. Näsänen, and K. Osmoviita, "Cortical magnification and peripheral vision," J. Opt. Soc. Am. A **4,** 1568–1577 (1987).
7. J. S. Pointer, "The cortical magnification factor and photopic vision," Biol. Rev. **61,** 97–119 (1986).
8. H. Strasburger, L. O. Harvey, and I. Rentschler, "Contrast thresholds for identification of numeric characters in direct and eccentric view," Percept. Psychophys. **49,** 495–508 (1991).
9. L. O. Harvey and E. Pöppel, "Contrast sensitivity of the human retina," Am. J. Optom. **49,** 748–753 (1970).
10. I. Lie, "Visual detection and resolution as a function of retinal locus," Vision Res. **20,** 967–974 (1980).
11. C. A. Johnson, J. L. Keltner, and F. Balestrery, "Effects of target size and eccentricity on visual detection and resolution," Vision Res. **18,** 1217–1222 (1978).
12. M. Fahle and M. Schmidt, "Naso-temporal asymmetry of visual perception and of the visual cortex," Vision Res. **28,** 293–300 (1988).
13. M. E. Wilson, "Invariant features of spatial summation with changing locus in the visual field," J. Physiol. **207,** 611–622 (1970).
14. A. Johnston, "Spatial scaling of central and peripheral contrast-sensitivity functions," J. Opt. Soc. Am. A **4,** 1583–1593 (1987).
15. A. B. Watson, "Estimation of local spatial scale," J. Opt. Soc. Am. A **4,** 1579–1582 (1987).
16. P. Bijl, J. J. Koenderink, and A. Toet, "Visibility of blobs with a Gaussian luminance profile," Vision Res. **29,** 447–456 (1989).
17. F. W. Weymouth, "Visual sensory units and the minimal angle of resolution," Am. J. Ophthalmol. **46,** 102–113 (1958).
18. P. Bijl and J. J. Koenderink, "Visibility of elliptical Gaussian blobs," submitted to Vision Res.
19. C. W. Tyler, "Analysis of visual modulation sensitivity. III. Meridional variations in peripheral flicker sensitivity," J. Opt. Soc. Am. A **4,** 1612–1619 (1987).
20. The stimulus and the background are generated with 8-bit precision. Therefore $L(r, t)$ is physically indistinguishable from the background luminance for $r > 4\sigma_s$ or $|t - t_0| > 4\sigma_t$.
21. P. Bijl and J. J. Koenderink, "Model for spatio-temporal contrast detection," Biol. Cybern. (to be published).
22. J. M. Valeton and A. B. Watson, "Contrast detection does not have a local spatial scale," Invest. Ophthalmol. Vis. Sci. Suppl. **31,** 428 (1990).
23. H. Wässle, U. Grünert, J. Röhrenbeck, and B. Boycott, "Retinal ganglion cell density and cortical magnification factor in the primate," Vision Res. **30,** 1897–1911 (1990).
24. R. A. Linsenmeier, L. J. Frishman, H. G. Jakiela, and C. Enroth-Cugell, "Receptive field properties of X and Y cells in the cat retina derived from contrast sensitivity measurements," Vision Res. **22,** 1173–1183 (1982).